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The diet of the Crested porcupine *Hystrix cristata* L., 1758 in a Mediterranean rural area

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Abstract

Studied was the diet of crested porcupines by faecal analysis in a rural hilly area in central Italy. Food categories were identified by comparison with either isolated sections of fresh plant material or digested fragments obtained from captive porcupines fed experimentally. Roots predominated in the diet and were consumed at a similar frequency all year round. Herbs were the most eaten epygeal category especially in winter and spring. Possibly the winter consumption of herbs was related to a decrease in the availability of other food categories, such as grass inflorescences and fruits. Consumption of these two food categories was positively correlated and inversely associated with herbs. Grass inflorescences (mainly *Hordeum murinum*) were an important diet component in summer. Porcupines fed on fruits mainly in summer and autumn. The consumption of storage organs increased in winter and in spring. The values of trophic niche breadth and overlap suggested that porcupines are generalist foragers. These feeding habits, combined with the abandonment by man of the countryside in the last few decades, may partly explain the recent range expansion of the crested porcupine in Italy.

Introduction

The crested porcupine *Hystrix cristata* is a large rodent widely distributed in Africa, while in Europe it is present only in Central and Southern Italy, recently expanding its range northward and eastward (Pellegrini et al. 1991; Amori and Angelici 1992; Lovari 1993). Since 1974 it has been protected by the Italian law, but poaching for meat is still widespread. Crested porcupines are active all year round, mainly at night and spend most daylight hours in natural caves or burrows (Pigozzi and Patterson 1990; Corsini et al. 1995). Detailed information on diet of porcupine is scanty, often anecdotal and mainly based on non-systematic observations of feeding activity. Santini (1980) reported that porcupines use especially hypogeal parts (taproots, bulbs, tubers and rhizomes) of wild and cultivated plants. They also eat seeds, fruits, sprouts and green vegetation on the ground. In the Maremma Natural Park, Western Tuscany, Italy, porcupines fed on grain and sunflower seeds, as well as underground organs and grasses (Pigozzi and Patterson 1990: samples for July only). Porcupines have been reported to debark young trees, e. g. *Fraxinus ornus*, *Ficus carica* and conifers in winter (Santini 1980; Tinelli and Tinelli 1988, in the Maremma Natural Park; Zavalloni and Castellucci 1991, in the North-eastern Italian Apennines).

The aims of our research were to set up a technique for analysis of crested porcupines' faeces and to study the monthly/seasonal variation of the diet (in terms of plant parts) in a Mediterranean rural area.

Material and methods

Study area

The study was carried out in a 750 ha rural hilly area in Siena county, Tuscany, Italy (200–388 m a.s.l.), from July 1990 to June 1991. Temperature and precipitation are shown in Figure 1. The soils are mainly Miocene and Pliocene clays, sandstones and lacustrine conglomerates (Lazzarotto and Mazzanti 1976). Oakwoods cover 48.9% of the area, with *Quercus cerris* and *Q. pubescens* being the main species, with some *Acer campestre*, *Fraxinus ornus*, *Carpinus betulus* and *Juniperus communis.* Various trees and shrubs, mostly belonging to the Rosaceae, make up hedges (4.9%): *Prunus spinosa* often forms very thick bushes, while *Rosa canina*, *Pyrus pyraster*, *Malus sylvestris*, as well as *Spartium junceum*, *Cornus mas* and *Robinia pseudoacacia* are also present. Interspersed fields cover 38.8% of the study area; they are set aside (according to EEC programs), but a few of them are used as sheep and cattle pasture. Grasses (*Avena fatua*, *Bromus* spp. and *Hordeum murinum*) predominate in the fields, and, among forbs, *Rumex crispus* and *Rumex conglomeratus* are very frequent species. Names of plant species according to Pignatti (1982).

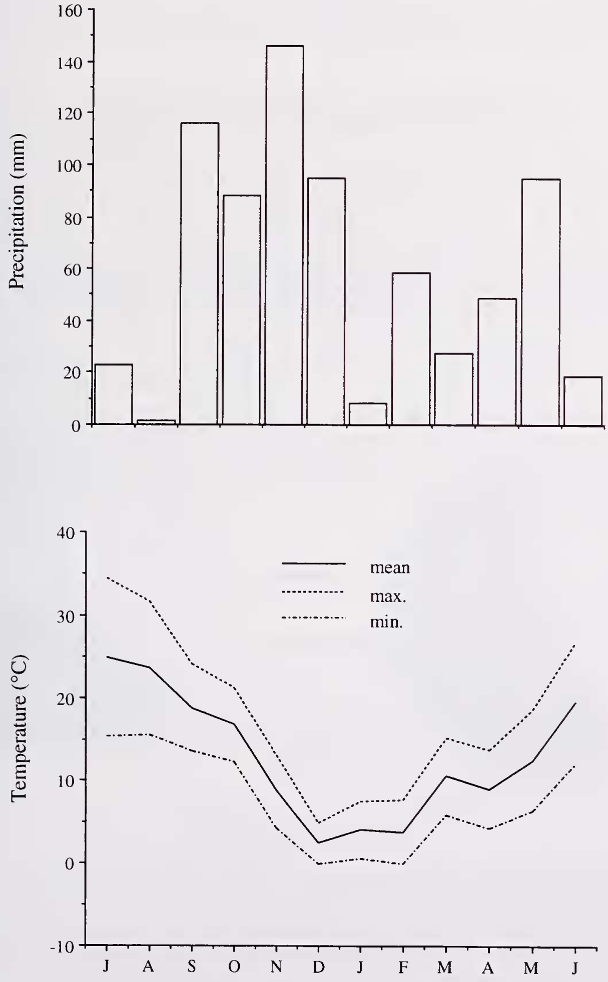

Fig. 1. Monthly precipitation and mean temperature during the study period.

Diet analysis

Droppings were collected weekly on fixed routes from July 1990 to June 1991. The samples were stored in plastic bags and frozen. A monthly mean of 9.3 (range: 5–11) droppings (a total of 111 samples) was analysed.

Each sample was dipped in a 0.06 M NaOH solution (e.g. ZYZNAR and URNESS 1969; ORMEROD 1985) for about 24 hours, to dissolve the mucous coat covering the faeces; then it was washed through a 1 mm square mesh sieve (Endecotts Ltd.) (HOLECHECK 1982; GARCIA-GONZALEZ 1984; CHAPUIS and DIDILLON 1987). The washed sample was placed in water and the fragments were segregated by hand, according to the food categories they belonged to. They were identified either by eye or by using a stereomicroscope at 25× to 125× magnification, by comparison with either digested fragments obtained from experimental meals or isolated sections of bulbs and tubers of Liliaceae, Araceae and Iridaceae occurring in the study area. Leaves and stems of herbs could be identified as either Monocotyledons or Dicotyledons by eye. When not large enough, leaf fragments were distinguished under a dissecting microscope at 100× magnification on the basis of epidermal diagnostic features such as venations and stomata, typically arranged in parallel lines only in Monocotyledons. Grass inflorescences were identified to species by comparison with herbarium specimens. In the fruits category, seeds, peel, pulp fragments and petioles were found. Volume was measured by water displacement (e. g. JACKSON 1980; STAINES et al. 1982; MARTINEZ et al. 1985). Volumes less than 0.1 ml were recorded as "traces". This procedure actually measures the volume of indigestible food remains, so the resulting data must be interpreted with caution.

Feeding experiments with captive porcupines

Adult porcupines, held in outdoor enclosures, were fed experimental meals to obtain reference faecal samples of food categories, such as: a) taproots of herbs, b) fruits of shrubs and trees and c) bark of shrubs and trees. Experimental meals were composed of plant species sampled in the study area. On the three days preceding each test, porcupines were maintained on ad libitum water and not fed, so only indigested remnants of the food given them should have been included in faecal samples. On the day of test, all accumulated faeces were removed from the enclosure and the animals were fed the experimental meals. Faeces were collected each following day, until 2–3 days after the last experimental meal had been eaten.

Porcupines were offered taproots of herbs (*Rumex* spp., *Linaria vulgaris*, *Amaranthus retroflexus*, *Tussilago farfara* and *Inula viscosa*) in experiment a (eight days) and fruits of *Pyrus pyraster*, *Malus sylvestris*, *Sorbus domestica*, *Prunus* spp., *Rosa canina* in experiment b (twelve days). Experiment c needed to be carried out twice, because porcupines did not eat stripped tree bark (*Quercus cerris*, *Acer campestre*, *Ulmus minor*, *Prunus spinosa*). Therefore, in the second trial, porcupines were offered a bunch of branches of the same tree species fastened to the enclosure. Parts of the branches were then eaten. This experiment lasted three days.

Statistics

Data for each month were analysed as:

1. Percent frequency of occurrence for each food category:

$$OF_{ij}\% = n_{ij}/N_j \times 100$$

where OF_{ij} % is the percentage of faeces in which the i_{th} category occurs in the j_{th} month; n_{ij} is the number of times in which the i_{th} category occurs in the j_{th} month out of the total of frequencies of all the food categories in the j_{th} month (N_j).

2. Percent volume of each food category:

$$V_{ij}\% = \Sigma v_{ij}/\Sigma V_j \times 100$$

where V_{ij} % is the percent volume of the i_{th} category in the j_{th} month; Σv_{ij} is the sum of volumes (ml) of the i_{th} category in the j_{th} month and ΣV_j is the total volume analysed in the j_{th} month.

The χ^2 test for one sample was used to evaluate differences in the annual occurrence frequency of food categories. To estimate the association level between monthly frequency of occurrence and both monthly mean temperature and precipitation we applied the Spearman rank correlation coefficient (SIEGEL and CASTELLAN 1988). This test was used also to evaluate monthly statistical associations between food categories. No inter-category statistical comparisons were made on volume data because of the possible different rates of digestibility of different plant parts. To compare seasonal compositions of diet (in terms of occurrence frequency), monthly data were combined in groups of three (e. g., winter was made up of data from January, February and March) and the χ^2 test for two independent samples was applied. We cannot exclude some dependence of our samples because faeces might belong to the same individual/s. Nevertheless, we would regard our tests as significant even in case of some level of sample dependence, because of the very high levels of significance obtained (see Tabs. 2–3).

Monthly trophic niche breadth was estimated by the standardized Levins index (B_{sta}) (Colwell and Futuyma 1971):

$$B_{sta} = B - 1 / B_{max} - 1$$

where B is the Levins index and B_{max} is the total number of food categories composing the diet. The value of B_{sta} varies from 0 (the smallest niche breadth) to 1 (the largest niche breadth). The Levins index formula (Levins 1968) is:

$$B = 1/\sum_{i=1}^{n} p_i^2$$

where n is the number of food categories and p is the proportion (as frequency of occurrence) of the i_{-th} category. B varies from 1 to n.

Monthly trophic niche overlap was estimated by the Pianka index O (Pianka 1973):

$$O_{jk} = \Sigma p_{ij}\, p_{ik} / \sqrt{\Sigma p_{ij}^2 \Sigma p_{ik}^2}$$

where p_{ij} is the proportion (as frequency of occurrence) of the i_{th} category in the j_{th} month and p_{ik} is the proportion of the same category in the following k_{th} month. O varies from 0 (the smallest niche overlap) to 1 (the largest niche overlap).

Results

Fragments found in faeces were segregated in the following food categories: grass inflorescences; herbs; fruits; roots; storage organs; unidentified material. Since bark could not be distinguished from roots under the stereomicroscope in material obtained from experi-

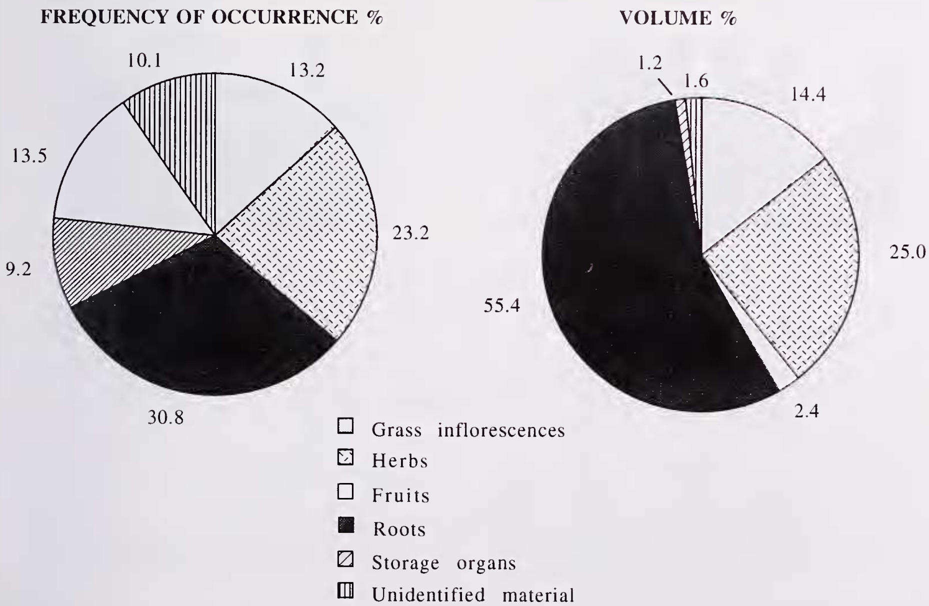

Fig. 2. Annual composition of diet in food categories.

mental meals, we cannot exclude the possibility that the roots category contained some bark fragments.

Annual diet

Roots constituted the main category in annual diet, both in frequency of occurrence and especially in volume (Fig. 2). Herbs ranked as the second food category, with similar values of occurrence and volume. Fruits and grass inflorescences were present with about the same frequency. Unidentified material made up a small portion of the analysed matter as both frequency and volume. Storage organs showed the smallest values of frequency and volume. Differences among food categories proved significant ($\chi^2 = 77.2$, d. f. = 5, $p = 0.0001$).

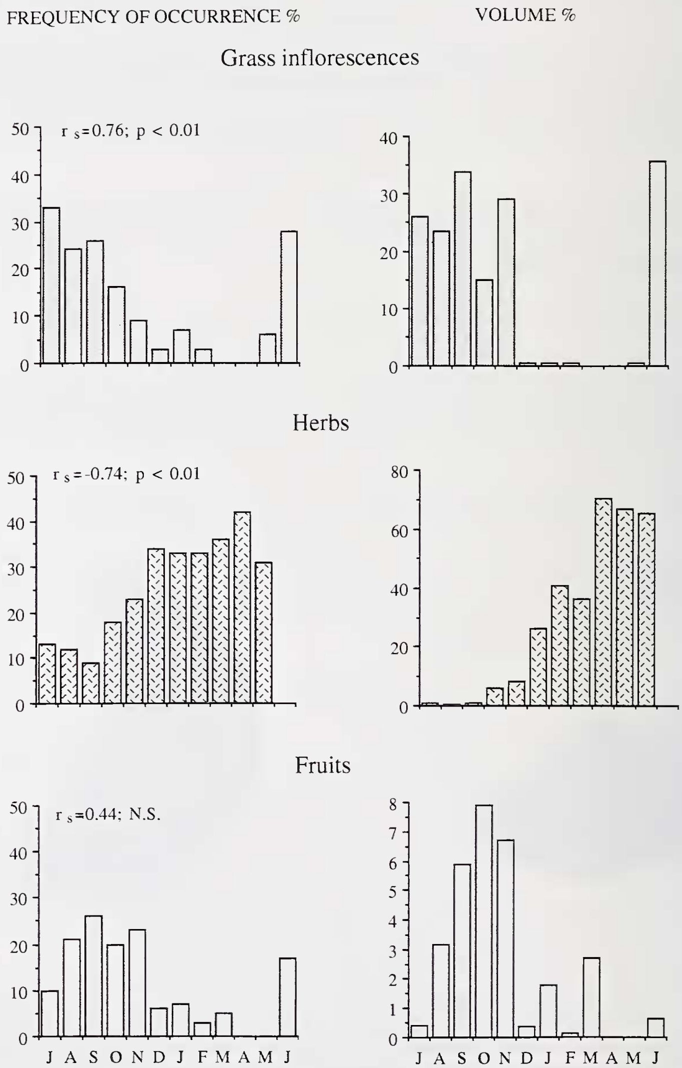

Fig. 3. Monthly percent frequency of occurrence and volume of epygeal food categories (r_s = Spearman 2-tailed rank correlation coefficient between occurrence frequency and monthly temperature; N = 12).

Monthly diet

As regards food categories made up by epygeal plant parts (Fig. 3), grass inflorescences showed the highest values of occurrence in summer months, while they tended to decrease from October to March and April, when this category disappeared, although it was present again in May. In terms of volume, grass inflorescences followed a similar trend, but their contribution to the diet from September to November was relatively higher. A positive correlation was found between the mean monthly temperature of the study area and the frequency of occurrence of this food category (Fig. 3). *Avena fatua*, *Bromus* spp. panicles and mainly *Hordeum murinum* spikes made up this category. On the contrary, herbs, negatively correlated to grass inflorescences (Tab. 1), showed the lowest values of

Table 1. Monthly correlations between food categories (r_s = Spearman 2-tailed rank correlation coefficient; N = 12; p = significance level)

Food categories	r_s	p
Herbs vs Grass inflorescences	–0.92	< 0.01
Fruits vs Herbs	–0.76	< 0.01
Fruits vs Grass inflorescences	0.72	< 0.02
Roots vs Grass inflorescences	–0.39	N. S.
Roots vs Herbs	0.56	N. S.
Roots vs Fruits	–0.50	N. S.
Roots vs Storage organs	–0,12	N. S.
Storage organs vs Herbs	0.03	N. S.
Storage organs vs Fruits	–0.36	N. S.
Storage organs vs Grass inflorescences	-0.05	N. S.

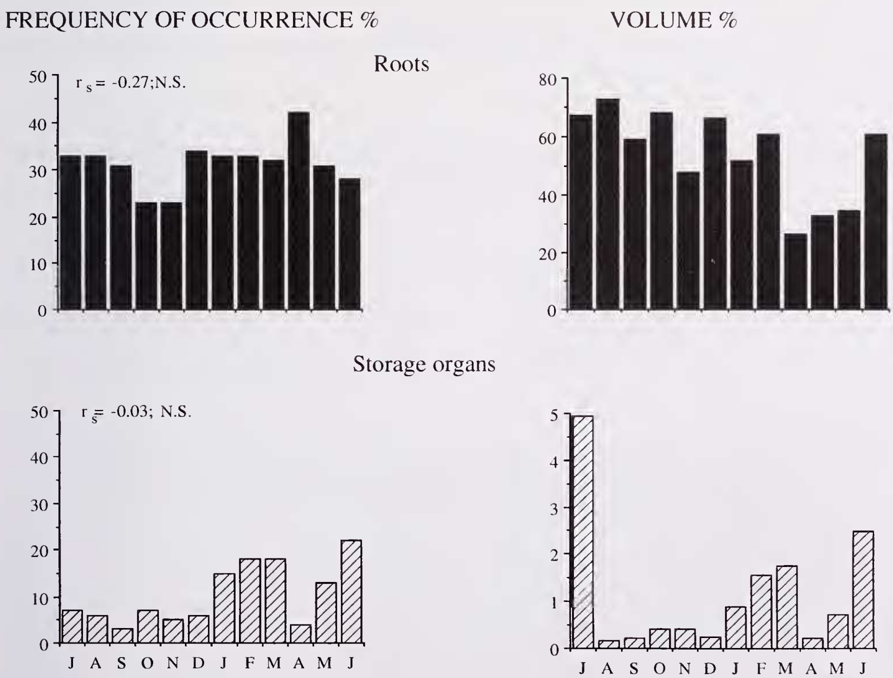

Fig. 4. Monthly percent frequency of occurrence and volume of hypogeal food categories (r_s = Spearman 2-tailed rank correlation coefficient between occurrence frequency and monthly temperature; N = 12).

frequency, as well as of volume, in the summer months and the highest ones from October to May. In June herbs surprisingly disappeared. The consumption of herbs was negatively correlated with temperature (Fig. 3). Dicotyledons disappeared from the diet of September and October, but occurred again in November, with increasing values to March, when they constituted more than 50% of the total herbs. Fruits, negatively correlated to herbs and positively to grass inflorescences (Tab. 1), were eaten mainly (both in terms of frequency and volume) at the end of summer to October and November. They were also consumed in winter months, but at lower values, and in April and May they did not occur at all but were again in the diet in June (Fig. 3). We could identify fruits of *Malus sylvestris* and *Pyrus pyraster*, very frequently in September and October, but only once (in September) we found one seed of *Cornus mas.*

As to food categories composed of hypogeal plant parts (Fig. 4), roots were consumed at a steady frequency all year round, but with varying quantity, showing the lowest relative volume from the end of winter to spring. Among root fragments we found taproot of *Rumex* spp. to be very frequent within this category (24% to 48% of total roots in summer and winter diet, respectively). Storage organs were made up of bulbs (particularly frequent in winter months); tubers of *Arum italicum*, occurring in July and in the winter months; corms of *Gladiolus italicus*, in August and May. On the whole, storage organs showed varying values in both frequency of occurrence and in volume, increasing in winter and again in spring months.

No food category showed significant correlations with monthly mean precipitation.

Seasonal diet

Seasonal compositions of diet proved significantly different at χ^2 test (Tab. 2). To explain which food category/ies caused these significant differences, we applied the χ^2 test to seasonal values of frequency of occurrence and volume of each category (Tab. 3). Roots and storage organs were the only food categories whose frequency of occurrence and volume, respectively, did not vary significantly from season to season.

Table 2. Comparisons of seasonal composition of diet (χ^2 = chi square test values, d. f. = 5; p = significance level)

Seasons	χ^2	p
Summer vs Autumn	47.9	0.0001
Autumn vs Winter	68.6	0.0001
Winter vs Spring	11.0	0.005
Spring vs Summer	85.4	0.0001

Table 3. Seasonal comparisons of each food category (χ^2_{OF}, χ^2_V = chi square test values applied to occurrence frequency and volume, respectively; d. f. = 3; p = significance level)

Food category	χ^2_{OF}	p	χ^2_V	p
Grasses inflorescences	24.43	0.0001	63.70	0.0001
Herbs	11.80	0.01	71.40	0.0001
Fruits	15.50	0.001	8.04	0.04
Roots	1.41	N. S.	44.06	0.0001
Storage organs	9.56	0.03	2.84	N. S.
Unidentified material	9.06	0.02	8.70	0.03

Trophic niche breadth and overlap

Monthly breadth of porcupine trophic niche was variable, with the largest values in the autumn and the smallest ones from late autumn to late winter. Monthly trophic niche overlap proved steady and large all year round. Diet overlap level decreased to smaller values only between May and June (Fig. 5).

Fig. 5. Monthly trophic niche breadth and overlap values (B_{sta} = standardized Levins index; O = Pianka index).

Discussion

Our study showed that the crested porcupine is not only a consumer of hypogeal, but also of epygeal plant parts e. g. grass inflorescences, fruits and especially herbs. *Hystrix indica* has been observed eating green grass in the coastal plain of Israel (SEVER 1985). In the desert *H. indica* mostly forages on below-ground plant organs (GUTTERMAN 1982; ALKON and OLSVIG-WHITTAKER 1989), reflecting the abundance of geophytes relative to other plants in such an environment. In our research above-ground vegetation was a more important part of the porcupine diet, reflecting higher availability of fresh nutrient herbs in our study area. Roots were used with the highest frequency all year round, even if sometimes in relatively small quantities, e. g. in some spring months. They constituted, together with storage organs, an important component of the diet, showing no significant seasonal differences in their consumption. In fact, hypogeal parts of perennial plants are a continually-available food resource. They were mostly *Rumex* spp. taproots, which were apparently very abundant in our study area. We observed several diggings of porcupine with fragments of *Rumex* spp. plant, as well as with *Allium* spp. The consumption of *Arum italicum* tuber was surprising, since this genus is known to be toxic, at least to domestic animals (VERONA 1984). Debarking activity has been recorded for *Erethizon dorsatum* (TENNESON and ORING 1985) and *Hystrix indica* (SHARMA and PRASAD 1992). In Italy, it has been noticed in areas where *H. cristata* occurs, but debarked trees or shrubs were never observed in our study area. Considering also the difficulty we found in making captive porcupines feed on bark, we suggest that, in our study area, bark is not an important food resource.

As regards its feeding behaviour, the porcupine is reported as a generalist (SANTINI 1980). Its diet would therefore be expected to vary in relation to availability of numerous vegetable food resources, which in turn depend on environmental variables (e. g. CAVALLIni and Lovari 1991; Lucherini et al. 1991; Lovari et al. 1994 for Mediterranean habitat). Our analysis showed seasonal variations in the consumption of epygeal plant parts. The direct correlation between the frequency of grass inflorescences in the porcupine diet and the temperature suggested a consumption of this food category proportional to its availability: the peak of consumption was in summer months, when flowering occurred, but this category was not found in the early spring diet, when environmental availability of grass inflorescences is expected to be very low. The consumption of herbs was complementary to that of grass inflorescences, being very high in early spring (possibly reflecting a use proportional to the seasonal availability) and in winter, when their consumption could suggest an active search for them by the porcupines. On the other hand, the probable winter decrease in the availability of nutritious epygeal food categories, could have constrained porcupines to choose herbs. The autumnal peak of fruits in diet probably reflected their abundance on trees and, consequently, on the ground, where porcupines had access to them. Moreover, the changing seasonal availability of this diet component, together with that of grass inflorescences, was likely compensated by feeding on herbs.

The variable levels of trophic niche breadth supported further the hypothesis that the crested porcupine adopts a generalist feeding behaviour: it consumes hypogeal plant parts, fruits and grass inflorescences with a frequency reflecting their availability in the study area and uses herbs with a pattern apparently compensating the seasonal variations of food resources. The small niche breadth observed from winter to early spring could be caused by a decreased availability of food resources. Alternatively, it might be accounted for by an active selection of a few highly-preferred food categories. We think that this second hypothesis is less probable, because of the winter dormancy of vegetation. The high level of trophic niche overlap all year round, accounted for by the high monthly proportion of roots, indicated quite a homogeneous composition of the diet.

Its ability to feed on the most abundant food resources in its habitat makes this rodent a potential cause of crop damage, especially where it occurs at high density. On the other hand, olives and grapes, cultivated in the study area, were never found in porcupine faeces, although fragments of other fruit tree seeds were identified. Furthermore, no cases of feeding by porcupines in house-gardens have been reported.

Thus, the recent spread of the range of *H. cristata* in Italy can be accounted for by the wide ecological tolerance common to the *Hystrix* genus (e. g., Sever and Mendelssohn 1988 for *H. indica*; Haim et al. 1990 for *H. africaeaustralis*) and, particularly, by the generalist feeding behaviour found in this study combined with the abandonment by man of the countryside in the last few decades.

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Zusammenfassung

Die Zusammensetzung der Nahrung des Nordafrikanischen Stachelschweines (Hystrix cristata L., 1758), in einem mediterranen, ländlichen Habitat

Die Zusammensetzung der Nahrung des Nordafrikanischen Stachelschweines wurde in einem ländlichen, hügeligen Gebiet Mittelitaliens durch Kotanalysen untersucht. Nahrungsgruppen wurden sowohl durch den Vergleich von Proben aus frischem Pflanzenmaterial als auch von verdautem Material von in menschlicher Obhut gehaltenen, experimentell gefütterten Stachelschweinen identifiziert. Wur-

zeln waren vorherrschend und wurden das ganze Jahr hindurch in ähnlichem Ausmaß aufgenommen. Kräuter, negativ korreliert mit der Lufttemperatur, stellen die von den oberirdisch wachsenden Pflanzenteilen am häufigsten aufgenommene Pflanzengruppe dar, vor allem im Winter und im Frühling. Die winterliche Aufnahme von Kräutern war möglicherweise durch die Abnahme des Angebots an anderen Pflanzengruppen bedingt, z. B. an Blütenständen der Gräser und an Früchten. Die Aufnahme von diesen beiden letztgenannten Futtergruppen war positiv korreliert und umgekehrt korreliert mit der Aufnahme von Kräutern. Blütenstände der Gräser waren wichtige Futterbestandteile im Sommer, und deren Aufnahme war positiv mit der Temperatur korreliert. Stachelschweine nahmen Früchte besonders im Sommer und im Herbst auf. Die Aufnahme von unterirdischen Pflanzenteilen stieg im Winter und im Frühjahr an. Die Breite der Nahrungsnische und deren Überlappung weist darauf hin, daß es sich bei den Stachelschweinen um Futtergeneralisten handelt.

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